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Differentiation of *Xiphocolaptes* (Dendrocolaptidae) across the river Xingu, Brazilian Amazonia: recognition of a new phylogenetic species and biogeographic implications

by José Maria C. da Silva, Fernando C. Novaes & David C. Oren

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The genus *Xiphocolaptes* encompasses several of the largest (> 100 g) species of forest and woodland woodcreepers in the Neotropical region. The species with the largest geographical range in the genus is the highly variable Strong-billed Woodcreeper *X. promeropirhynchus*, found from Mexico to Bolivia (Peters 1945). Within this range, 23 subspecies are recognized (Peters 1945). Cory & Hellmayr (1925) suggested that the subspecies of *X. promeropirhynchus* can be grouped into two species: *X. promerophyrhynchus*, the highland group, occupying Central America, mountains of northern Venezuela, Colombia, Ecuador, Peru and Bolivia; and *X. orenocensis*, the lowland group, restricted to the Orinoco and Amazon basins. Although this arrangement was accepted by some authors (e.g., Gyldenstope 1951), it has not been followed by most recent taxonomists (e.g. Zimmer 1934, Peters 1945, Pinto 1978, Meyer de Schauensee 1978, Sibley & Monroe 1994). Ridgely & Tudor (1994) stated that it is premature to split *orenocensis* and *promeropirhynchus* without additional study, although they indicated that there is an altitudinal gap between the two forms along parts of the eastern slope of the Andes.

According to Hellmayr (1925), Peters (1951), Pinto (1978) and Ridgely & Tudor (1994), the *orenocensis* group is composed of six taxa: *orenocensis* (southern

Venezuela, eastern Ecuador, northern Peru and western Brazil, north of the Solimões), *neblinae* (Venezuela: Amazonas, Cerro de la Neblina), *tenebrosus* (Venezuela: western slope of the Mt. Chimantá-tepui and base of Mt. Roraima), *obsoletus* (Eastern Bolívia, Depto. Santa Cruz); *berlepschi* (eastern Peru and western Brazilian Amazonia, south of Solimões to the left bank of the Madeira); and *paraensis* (Brazilian Amazonia, south of the Amazon between the Madeira and Tapajós rivers). No contact between two subspecies of the *orenocensis* group is known. This could be a consequence of the lack of detailed information about the range limits of these taxa, a common problem in neotropical ornithology (Oren & Guerreiro 1994, Silva 1995a), but it is also possible that the ranges of these subspecies are effectively separated by major geographic barriers, such as mountains (*neblinae* and *tenebrosus*) or some of the largest Amazonian rivers (all remaining taxa).

Most of the taxa included in the *orenocensis* group are diagnosable by an unique combination of plumage characters (Hellmayr 1925, Zimmer 1934, Todd 1948, Zimmer & Phelps 1948, Phelps & Phelps 1955). Thus, they could be regarded as good candidates to be ranked as species under the phylogenetic species concept (Cracraft 1983, 1997). The major taxonomic puzzle within this group is the status of *neblinae*, a taxon based on a single specimen from Cerro de la Neblina on the Venezuelan-Brazilian border (Phelps & Phelps 1955) which, in spite of concentrated research effort in the same area, has not been collected again, although it was seen once (Willard *et al.* 1991).

Until recently, the eastern limit of the genus *Xiphocolaptes* in Amazonia was considered to be the western bank of the river Xingu. During our studies of the birds of the Serra dos Carajás (06º00'S, 51º 20'W), a plateau region (300-800 m) located between the rivers Xingu and Tocantins/Araguaia, two specimens of a new population of *Xiphocolaptes* were collected in 1985 and 1986. Graves & Zusi (1990) recorded two further specimens of this population collected 52 km SSE of Altamira, east bank of the river Xingu (03º39'S, 52º22'W) in 1986. We located another specimen in the ornithological collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP 65866), that was collected by J. Hidasi at Itupiranga (05º09'S, 49º20'W), Pará, on 11 June 1967. Finally, another specimen was collected by J. Roma, M. Henriques and D. Pimentel at São João do Araguaia, Serra das Andorinhas (06º09'S, 48º42'W), Pará, on 31 August 1995.

In this paper, we compare the plumage and body measurements of the specimens of *Xiphocolaptes* collected between the rivers Xingu and Tocantins/Araguaia with specimens collected between the rivers Tapajós and Xingu to determine if this recently discovered population represents a new taxon within the *orenocensis* group, or if it is *paraensis*, the geographically closest relative. In addition, we suggest that the region between the rivers Xingu and Tocantins/Araguaia should be ranked as a centre of endemism for the South American avifauna. Finally, we discuss why the Belém Centre, unlike other Amazonian centres of endemism, has no large woodcreeper of the genera *Hylexetastes* and *Xiphocolaptes*.

Methods

We obtained data from all known specimens of the recently discovered population. We compared these specimens with those of the geographically closest relative, *paraensis*. Specimens are housed at the National Museum of Natural History (NMNH), Carnegie Museum of Natural History (CM), Museu Paraense Emílio Goeldi (MPEG), and Museu de Zoologia da Universidade de São Paulo (MZUSP).

Plumage characters were described according to Smithe (1975, 1981). Where possible, the following body measurements were taken for each specimen: wing length (flattened); tail length; total culmen (bill length measured from the insertion of the bill to skull to the tip); bill from nostril (bill length measured from the anterior edge of the nostril to the tip of the maxilla); and tarsus length. To evaluate if there is a significant difference in body measurements across the river Xingu, males (the number of female specimens was too small for any comparison) of the recently discovered population and *paraensis* were compared. Body measurements ($\log_{10}$-transformed) were compared using t-tests. We generated a linear discriminant function to evaluate whether specimens of the new population and *paraensis* are separated correctly, based only on body measurements. All statistical tests were made using SYSTAT 7.0.

Results

Plumage variation

The population between the rivers Xingu and Tocantins/Araguaia shares several plumage characters with *paraensis,* such as the general plumage pattern as well as tail, rump, wing, upper-parts and crown colour. However, there are important differences in the colouration of the under-parts, in the width and colour of the upper-part streaks, and on the stripe width in the pileum and head. These characteristics were not variable in the specimens we examined.

Body measurements

Apart from bill from nostril, all body measurements of males of the new population and of *paraensis* are significantly different (Table 1). In general, the specimens of the new population are significantly smaller than those of *paraensis* (Table 1). Between specimens of the new population and *paraensis*, there is no overlap in wing, tail, and total culmen measurements, a small overlap in tarsus, and extensive overlap in bill from nostril (Table 1). By combining all body measurements in a linear discriminant function, the individuals of the two groups are 100% correctly classified.

Description of the new taxon

All specimens of the recently discovered population of *Xiphocolaptes* from the region between Xingu and Tocantins/Araguaia can be easily separated from the specimens of *paraensis*, based on both plumage characters and body measurements. Both suites

of characters have a discontinuous variation across the river Xingu, as one could expect if these characters were result of genetic-environmental interactions (Barrowclough 1982). Based on this assessment, we propose that the specimens from the region between the rivers Xingu and Tocantins/Araguaia represent a new phylogenetic species, which we name:

Xiphocolaptes carajaensis sp. nov., Carajás Woodcreeper

Holotype. MPEG 38284, male (skull 100% ossified; testes 6 x 3 mm; no bursa), collected 21 July 1986 by José Maria Cardoso da Silva and Manoel Santa Brígida at Caldeirão, Serra dos Carajás (06º00'S, 51º 20'W), municipality of Parauapebas, Pará, Brazil.

Diagnosis. Similar to *X. paraensis* from Santarém, the geographically nearest phylogenetic species, but differs by the under-parts Clay Color (#26) rather than Antique Brown (#37), upper-parts with narrower and less conspicuous streaks, significantly shorter wing, tail and bill (Table 1) and, on average, narrower streaks on crown and head (Figure 1).

Description of the holotype. Black pileum with rachis Clay Color (#26); upperparts Cinnamon-Brown (#33); rump Hazel (#35); tail upper surface Chestnut (#32); throat whitish; breast Clay Color (#26) with the streaks Pale Horn (#92) bordered with Grayish Horn (#91); flanks Clay Color (#26); belly Pale Horn (#92) with small dark interrupted bars; undertail coverts Buff (#124) with bars Grayish Horn (#91); underwing coverts Pale Horn (#92) with Olive-Brown (#28) bars. Undersurface of the remiges Cinnamon-Rufous (#40). Iris red, maxilla black, mandible grey with dark spots in the distal parts; tarsi greenish.

***Measurements** (mm) of the holotype*. Bill from nostril 29.2, culmen 37.7, wing 125.0, tail 115.0, tarsus 30.2, Mass 114.0 g.

Paratype. MPEG 37216, collected by Manoel Santa Brígida and Rosemiro Pereira 27 June 1985 at Manganês, Serra dos Carajás, municipality of Parauapebas, Pará, Brazil.

Measurements (mm) of the paratype. Culmen 51.0, bill from nostril 38.5, wing 127.0, tail 113.2, tarsus 31.6 mm.

Etymology. The name is derived from the region (Serra dos Carajás) where the holotype was collected.

Habitat. At the Serra dos Carajás, the new taxon was collected and recorded in both tall mature terra firme forest (Manganês) and riverine várzea forest (Caldeirão). At both sites, only two individuals were recorded, even though intensive efforts were directed at these sites.

Specimens examined. *Xiphocolaptes carajaensis*. Brazil, Pará: Serra dos Carajás, Caldeirão (MPEG, 1 male, holotype) and Manganês (MPEG, 1 male, paratype); Itupiranga (MZUSP, 1 male); Xingú (NMNH, 1 male and 1 female); São João do Araguaia (MPEG, 1 male). *Xiphocolaptes paraensis*. Brazil, Pará: Lago Batista (3

TABLE 1
Comparisons of the measurements of *Xiphocolaptes paraensis* and *X. carajaensis*. Data are: range, mean ± standard deviation (n).

Measurements	*X. paraensis*	*X.carajaensis*	t-test
Wing	134.0-151.0, 142.8±6.2 (9)	121.0-129.0, 126.1±3.0 (5)	t_{12}=5.8, p<0.001
Tail	121.0-128.0, 125.4±2.8 (6)	108.0-115.0, 111.4±3.2(4)	t_{8}=7.2, p<0.001
Culmen	51.2-59.5, 55.1±2.7(8)	46.6-51.0, 49.4±1.8(5)	t_{11}=4.2, p<0.01
Bill from nostril	36.0-47.9, 40.2±3.4(8)	32.7-38.5, 36.6±2.4(5)	t_{11}=2.0, p>0.05
Tarsus	30.5-35.3, 33.0±1.7(9)	28.4-31.6, 29.8±1.3(5)	t_{12}=3.5, p<0.01

males, including the holotype; 1 male immature); Estrada Santarém-Cuiabá, km 84 (MPEG, 2 males) and km 212 (MPEG, 1 male); Pará, Santarém (CM, 1 male; MZUSP, 1 ?), Colônia do Mojuí (CM, 1 male), and Apaci (CM, 1 female); Mato Grosso, Fazenda São José, Rio Peixoto de Azevedo (MPEG, 1 male).

Discussion

The status of the new phylogenetic species under the biological species concept

A comprehensive programme of conservation and sustainable use of the biological diversity of a region will depend on having all taxonomically distinct, diagnosable populations identified and named. From this perspective, the species concept used by taxonomists has an important role (Cracraft, 1997). For instance, several methodologies to pinpoint priority areas for conservation and management (e.g., identification of areas with high number of endemic species or restricted-range species) may be influenced by how taxonomists recognise and delimit species. In ornithology, discussion on the species concept is becoming more frequent after more than 50 years dominated by the biological species concept [BSC; see McKitrick & Zink (1988) and Haffer (1992) for contrasting viewpoints].

An alternative to BSC is the Phylogenetic Species Concept (PSC): "a species is the smallest population or group of populations within which there is a parental pattern of ancestry and descent and which is diagnosable by unique combinations of character states" (Cracraft 1983). There are several reasons to use the PSC rather than BSC in studies on avian speciation, phylogeny reconstruction, geographic variation and biogeography (McKitrick & Zink 1988, Cracraft 1989). More recently, Cracraft (1997) listed several practical and theoretical reasons for using phylogenetic species rather than biological species in conservation biology.

Although ornithologists are moving toward the use of the phylogenetic species concept (Zink 1997), most current avian taxonomy is based on the biological species concept (Snow 1997). It is useful therefore to evaluate the status of the new phylogenetic species also under the framework of the biological species concept.

Although taxa comprising the *orenocensis* group are diagnosable and are not known to intergrade along their ranges, they should probably be grouped into a

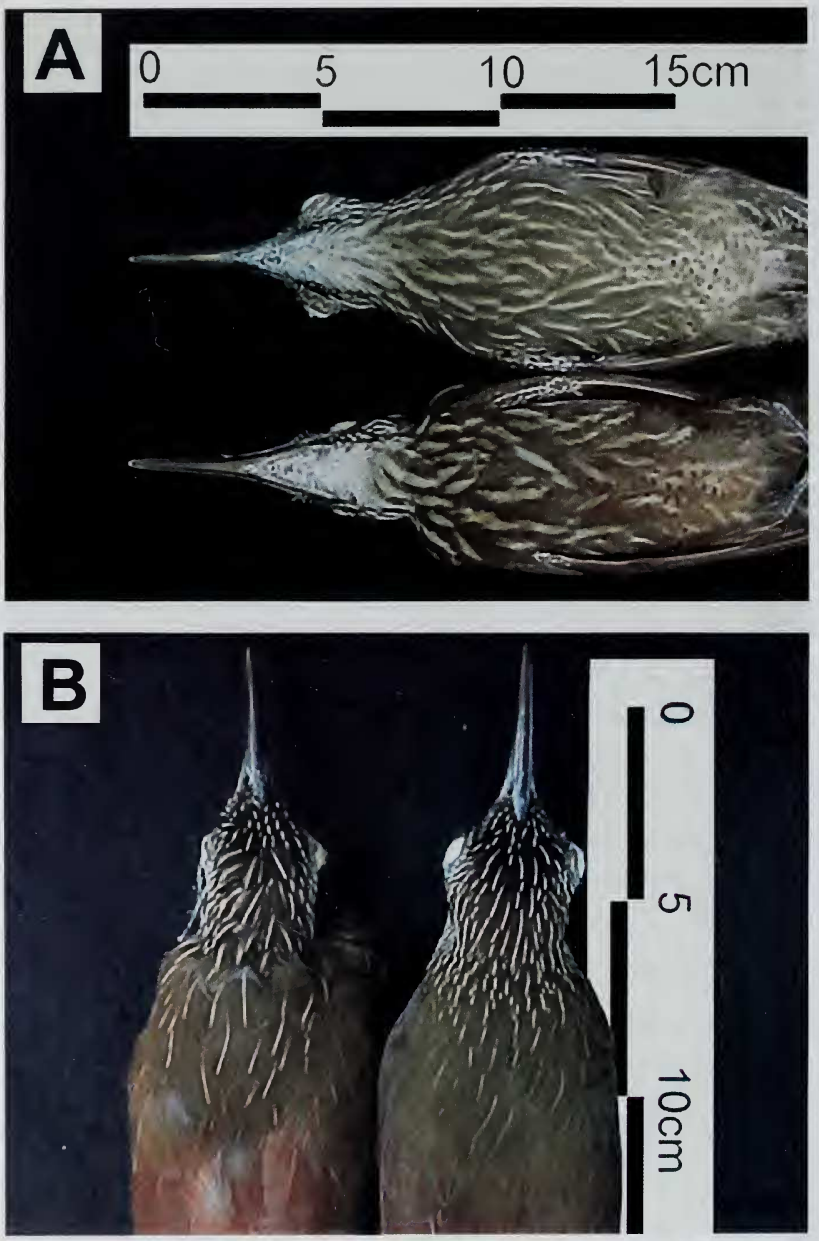

Figure 1. Differences between *Xiphocolaptes carajaensis*, from the region between rivers Xingu and Tocantins/Araguaia, and *X. paraensis*, from the region between rivers Tapajós and Xingu. (a) Ventral aspect: lower, *X. paraensis*; upper, *X. carajaensis*. (b) Dorsal aspect: left, *X. paraensis*; right, *X. carajaensis*.

single biological species, because the strong similarities in plumage colouration among close relatives may indicate a potential to interbreed if these taxa came into contact. At least at this stage of knowledge on the natural history and distribution of *Xiphocolaptes*, *X. carajaensis* should be ranked as a subspecies of *X. promeropirhynchus* or *X. orenocensis* under the biological species concept.

The region between the rivers Xingu and Tocantins deserves to be classified as an area of endemism for birds

In the most recent attempt to identify the South American avian centres of endemism, Cracraft (1985) recognized 33 centres, four of which are in the Amazonian forests south of the Amazon: South Amazon (Inambari) Centre, Rondônia Centre, Pará Centre and Belém (Maranhão) Centre. The region between the rivers Xingu and Tocantins/Araguaia was grouped with the region between the rivers Tapajós and Xingu into the Pará Centre (Figure 2).

Cracraft (1985) listed 20 taxa as endemic to the Pará Centre. Some of them (e.g. *Pipra pipra separabilis*) occur indeed on both banks of the Xingu, but others occur only on one bank (e.g. *Pipra vilasboasi*). Recent studies have led to several taxonomic discoveries in the region between the rivers Xingu and Tocantins/Araguaia, supporting the case for this region to be ranked as a distinct centre of avian endemism. Endemic taxa that support this suggestion include: *Psophia viridis interjecta*, *Pyrrhura perlata*

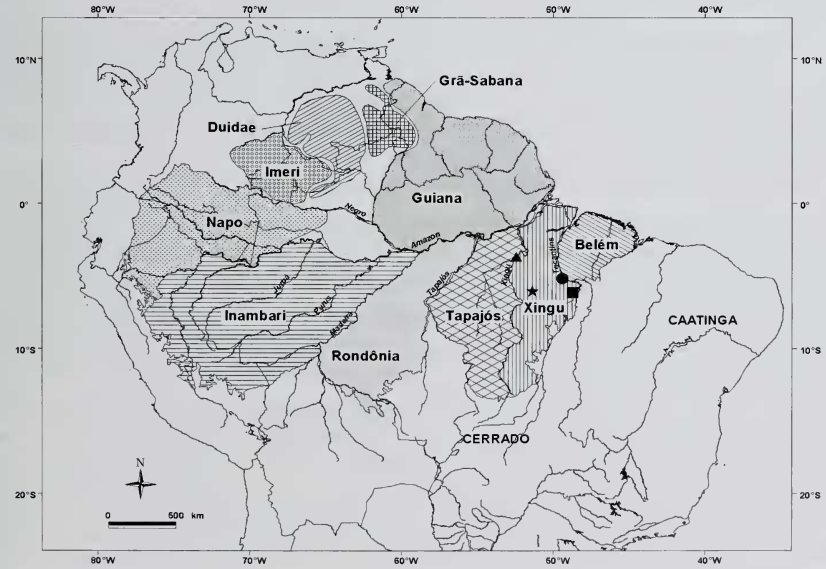

Figure 2. Distribution of *Xiphocolaptes carajaensis* in relation to avian areas of endemism identified for Amazonia. Duida and Grã-Sabana are sub-areas of endemism of the Panteupui area of endemism. Xingu and Tapajós areas were originally grouped into a single region named Pará. The localities of *X. carajaensis* are as follows: Serra dos Carajás (star), Xingu (triangle), Itupiranga (circle) and São João do Araguaia (square).

anerythra, *Hylexetastes brigidai*, *Xiphocolaptes carajaensis*, an undescribed phylogenetic species of *Dendrocincla* (Oren & Pinto-Henriques, unpublished), *Phlegopsis nigromaculata confinis*, *Pyriglena leuconota interposita*, *Conopophaga aurita pallida*, and *Procnias alba wallacei*.

An odd biogeographic pattern: why does the Belém Centre lack a large woodcreeper?

The largest woodcreepers in Amazonia are represented by species of *Xiphocolaptes* and *Hylexetastes*. At least one species of these two genera is recorded in the Amazonian areas of endemism, the exception being the Belém Centre. *Hylexetastes* occurs north and south of the Amazon, but is not known from the Belém Centre. *Xiphocolaptes* occurs in most of Amazonia, except the Guiana and Belém centres. This is an odd biogeographic pattern that deserves an explanation. Lack of a species in a region, in which it could be expected, might be due basically to three reasons: (a) the region is still poorly-sampled for birds; (b) ecological reasons; (c) historical reasons.

The Belém Centre is probably the Amazonian biogeographic region that has received the greatest attention from ornithologists during the last century (Oren & Albuquerque 1991). Although there are some areas of the Belém Centre that have never been sampled for birds, it is hard to imagine that the two largest woodcreeper genera in this entire region have simply been overlooked.

Hylexetastes and *Xiphocolaptes* might be absent from the Belém Centre because one or more essential ecological factors are lacking in this region. Differences in forest structure and composition, climate, likelihood of fires and the presence of potential competitors are some of the factors that might be suggested. However, none of them alone can explain this pattern well.

Finally, the absence of these genera from the Belém Centre might be due to historical reasons. Either these genera have never been in the Belém Centre, or they were present but have gone extinct. *Hylexetastes* is a genus endemic to Amazonia, with no representative outside this region. Thus, although we cannot rule out the hypothesis that *Hylexetastes* colonized and later went extinct in the Belém Centre, *Hylexetastes* may alternatively have never expanded its range towards the Belém Centre. This is not the case in *Xiphocolaptes*, which has a widespread range with at least one species in all major regions of tropical South America. In all centres of endemism around Belém (Guiana is the only exception), the genus *Xiphocolaptes* is represented: to the west, *X. carajaensis* is found; to the south-east, *X. falcirostris*, a bird associated with the dry forests of the Caatinga region, including part of Maranhão, occurs. Finally, *X. albicollis*, a species associated with Atlantic Forest, and that also inhabits the gallery forests of the Cerrado Region (Silva 1995b), is found south of the Belém Centre.

Based on this unexpected gap in its range, the absence of *Xiphocolaptes* in the Belém Centre is more parsimoniously explained by local extinction rather than any other hypothesis. There are some reasons to think that paleoecological dynamics could have caused several extinctions in the Belém Centre. Endler (1982) pointed

out that the Belém Centre is a peninsula of forest, isolated on one side by the Atlantic Ocean, and on two other sides by Cerrado and Caatinga. Because a peninsula of forest receives gene flow and dispersing individuals from fewer directions than do central populations with forest on all sides (Endler 1982), either differentiation in peripheral populations (Mayr 1963) or extinctions of large species with low densities, such as *Hylexetastes* and *Xiphocolaptes*, are amplified. This may result in areas of endemism that are characterized by both a number of endemic species and unexpected absence of some widespread taxa, such as the large Amazonian woodcreeper genera.

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Extension of the known range of the Red-shouldered Vanga *Calicalicus rufocarpalis* in southwest Madagascar

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Madagascar has been isolated from the African landmass for some 165 million years and, as a result, most of its plants and animals have evolved in isolation. Over 50% of Madagascar's breeding birds are endemic. Although our knowledge of the status and distribution of these species has improved in recent years, much basic information remains unknown. In particular, the species inhabiting the subarid thorn scrub of the far southwest of Madagascar have been little studied.

The Red-shouldered Vanga *Calicalicus rufocarpalis* was first described in 1997 (Goodman *et al.* 1997). This description was based on two females, collected from two locations near La Table, 13-20 km southeast of Toliara, in 1948 (Fig. 1). More recently, in 1991, a probable male was photographed at a nest 17 km southeast of Toliara, and in 1998 an expedition further south located birds at Vohombe, Lavavolo and Antsihanaka (ZICOMA 1999). These latter records represented the southern limit of the known range of the species. Following consultation with Frank Hawkins (BirdLife International) and experts from Projet ZICOMA (Zones d'Importance pour la Conservation des Oiseaux a Madagascar), it was decided to undertake a joint expedition to southwest Madagascar in 2000, to determine if the species was present in previously unsurveyed areas.